

1 **Changes in the distribution of Michigan crayfishes and the influence of invasive rusty**
2 **crayfish (*Faxonius rusticus*) on native crayfish substrate associations.**

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16 **Abstract:**

17 **Invasive crayfishes have a strong negative effect on multiple trophic levels, including**
18 **other crayfishes. However, documentation of the spread of non-native crayfish species and**
19 **their impact on native crayfishes could be improved, particularly over large spatial scales**
20 **in stream ecosystems. We collected crayfish and quantified habitat at 461 stream sites**
21 **throughout Michigan in 2014-2016 and compared our collections to a historical account of**
22 **crayfish collections published in 1975. Our objectives were to: 1) Quantify the change in**
23 **non-native rusty crayfish (*Faxonius rusticus*) and native species distributions from 1975 to**
24 **2014-16; 2) Quantify how rusty crayfish affect the habitat associations of native species in**
25 **Michigan streams; and 3) Determine the effectiveness of dipnets, our primary sampling**
26 **method. We found all species in more watersheds compared to 1975, likely due in part to**
27 **increased sampling. However, we found rusty crayfish in 22 more HUC-8 watersheds than**
28 **in 1975, a larger increase than all other species. Habitat associations of native species also**
29 **shift in the presence of rusty crayfish. In instances where native species co-occurred with**
30 **rusty crayfish, most obligate aquatic native species were found in less-preferred habitat**
31 **such as sand or macrophytes compared to cobble substrate when the species is in isolation.**
32 **Our results indicate a broad range expansion by rusty crayfish over the last 40 years,**
33 **suggesting that surveys of crayfish diversity and habitat occupancy should be more routine**
34 **to inform management of native crayfish species.**

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38 **Introduction:**

39 Invasions of non-native species represent one of the most important issues facing native
40 species biodiversity and ecosystem sustainability. Aquatic ecosystems are particularly
41 vulnerable to effects of invasions, and those systems that are prone to habitat modification or
42 disturbance are likely to be most susceptible to introductions of non-native species (Lozon and
43 MacIsaac 1997; Moyle and Light 1996). For the past few decades, scientists have debated the
44 relative roles of non-native species and habitat modification as engines of global change
45 (Didham et al. 2007; Didham et al. 2005). While some consensus has emerged that both play
46 important roles, synergies between non-native species introductions and habitat modification
47 represent a potent driver of ecosystem change. Crayfish invasions represent such a nexus. The
48 ability of crayfish to manipulate ecosystems has led them to be labeled ‘ecosystem engineers’
49 (Carreira et al. 2014; Hobbs et al. 1989; Lodge and Lorman 1987; Momot 1995; Momot et al.
50 1978). Further, the burrowing and foraging behavior of many crayfish species can alter both the
51 abiotic and biotic habitat available for native species through hydrologic alterations and
52 macrophyte habitat destruction, respectively (Faller et al. 2016; Wilson et al. 2004).

53 Crayfish invasions are often followed by extensive ecosystem disruption at a number of
54 trophic levels, from primary producers such as periphyton and macrophytes, to top predators
55 such as fishes (Carreira et al. 2014; Ilheu et al. 2007; Kershner and Lodge 1995; Lodge and
56 Lorman 1987; Roth et al. 2006; Roth et al. 2007; Wilson et al. 2004). Thus, there is considerable
57 interest in the distribution of crayfishes, particularly related to non-native species. The spread of
58 some crayfish species over broad spatial and temporal scales and their effects in the ecosystem
59 are well-documented, particularly for *Procambarus clarkii* in Europe (e.g. Gherardi 2006), but
60 the spread of most species has gone undocumented, at least over longer temporal scales (but see
61 Olden et al. 2006; Taylor and Redmer 1996).

62 Crayfishes can be a dominant component of freshwater ecosystems, but many species are
63 imperiled (Charlebois and Lamberti 1996; Huner and Lundquist 1995; Lodge et al. 1994;
64 Nystrom et al. 2006). In some aquatic ecosystems, crayfishes account for more biomass than all
65 other macroinvertebrates combined (Rabeni 1992). Crayfishes demonstrate a broad spectrum of
66 life history strategies, such as terrestrial burrowing, that allow them to persist in a wide variety of
67 habitats, including lakes, streams, wetlands, caves, and agricultural fields. These unique life
68 histories have allowed species to coexist by occupying distinct ecological niches depending on
69 seasonal water cycles or habitat heterogeneity (Hobbs 1942; Hobbs 1981; Welch and Eversole
70 2006). Nonetheless, crayfishes remain one of the most imperiled taxa in North America. As of
71 the mid-late 1990s, fewer than 50% of crayfish species populations were classified as stable
72 (Taylor et al. 1996; Wilcove et al. 1998). These estimates are likely conservative, as the most
73 recent comprehensive assessment is nearly 20 years old. Further, many species lack adequate
74 information on current distributions, habitat requirements, and threats to conservation that could
75 help prioritize conservation efforts. Substantial attention has been devoted to determining causes
76 of species replacements in crayfish communities related to differential susceptibility to predators
77 (DiDonato and Lodge 1993; Mather and Stein 1993a; Roth and Kitchell 2005), hybridization
78 with native species (Perry et al. 2001a; Perry et al. 2001b), and morphological or behavioral
79 differences among species (Bergman and Moore 2003a; Garvey and Stein 1993; Garvey et al.
80 1994; Gherardi and Daniels 2004; Pintor and Sih 2009), but less attention has been devoted to
81 changes in crayfish habitat selection following an invasion. Habitat selection associations of
82 native species often change in response to introductions of non-native species (Kiesecker and

83 Blaustein 1998; Losos et al. 1993; Trammell and Butler 1995), and previous studies document
84 that habitat is an important determinant of predation risk in crayfish (DiDonato and Lodge 1993;
85 Saiki and Tash 1979), and other species in aquatic and terrestrial ecosystems (Creel et al. 2005;
86 Hrabik et al. 2014; Valeix et al. 2009; Werner et al. 1983). Studies of crayfish species
87 distributions teamed with habitat surveys through time could inform our understanding of how
88 invasions affect native species, but many locales lack recent data on crayfish distributions (or in-
89 stream habitat) to perform such analyses.

90 A lack of recent crayfish distribution data is a significant concern in many locations.
91 Many states do not have updated crayfish distribution data, despite findings that indicate that
92 invasive crayfishes are one of the most common threats to native crayfishes (Lodge et al. 1998;
93 Lodge et al. 2000). For instance, Wisconsin and Illinois are the only states in the entire Great
94 Lakes Basin that have statewide crayfish surveys in the last 20 years (Olden et al. 2006; Taylor
95 and Redmer 1996). In the state of Michigan, addressing threats to native crayfish posed by
96 invasive species is a management priority. However, the last published comprehensive survey of
97 crayfishes in Michigan was from Creaser (1931), whom provided maps of crayfish collections
98 for individual species. However, these maps lack sufficient resolution to declare which
99 drainages some collections belong. In contrast, Lippson (1975) provides enough detail from their
100 crayfish collections throughout Michigan from the 1960s to provide us with an opportunity to
101 quantify changes in crayfish distributions from a more recent time, albeit from more than 40
102 years ago. Further, research on changes in native species behavior as it pertains to habitat
103 selection is relatively rare, particularly for non-native crayfish impacts on other crayfish species
104 with a few exceptions (Bergman and Moore 2003a; Jansen et al. 2009; Mather and Stein 1993b).
105 Herein, we document changes in the range of one non-native crayfish species (*Faxonius rusticus*)
106 across the State of Michigan, and quantify how habitat selection of native crayfish species differs
107 in streams where rusty crayfish are present compared to where they are absent.

108 Eight crayfish species are considered native in Michigan. Three are primarily found in
109 permanent open water habitats such as streams and lakes (*Cambarus robustus*, *Faxonius*
110 *propinquus*, and *Faxonius virilis*). Three use subterranean burrows (*Cambarus diogenes*,
111 *Cambarus polychromatus*, and *Creaserinus fodiens*) and are rarely observed in open water as
112 adults, except in spring and early summer when they release their young. Two are facultative
113 burrowers, depending on conditions such as precipitation and water levels in adjacent water
114 bodies (*Faxonius immunis*, and *Procambarus acutus*) (Hobbs and Jass 1988; Lippson 1975;
115 Thoma et al. 2005).

116 One non-native species of crayfish, the rusty crayfish (*F. rusticus*), has been reported in
117 Michigan for over 130 years with major range expansion occurring during the 20th Century
118 (Creaser 1931; Faxon 1884; Lippson 1975). The initial *F. rusticus* range expansion into the Great
119 Lakes basin is attributed to shipping canals connecting the Ohio River and Maumee River
120 watersheds in Ohio, and subsequent spread in the region is believed to be primarily a result of
121 bait bucket release by anglers or intentional release by lake managers seeking to manage
122 macrophyte communities (Creaser 1931; Olden et al. 2006). *F. rusticus* lives primarily in streams
123 and lakes and is observed to negatively affect populations of native stream and lake dwelling
124 crayfish, including the northern crayfish (*F. virilis*) and northern clearwater crayfish (*F.*
125 *propinquus*) (Garvey et al. 2003). Negative effects of rusty crayfish are numerous: a variety of
126 studies have demonstrated that they outcompete native species for food and shelter, exhibit less
127 susceptibility to native predators, and hybridize with native *F. propinquus* (Capelli and Munjal
128 1980; Capelli and Munjal 1982; Hill et al. 1993; Perry et al. 2002; Perry et al. 2001b; Roth and

129 Kitchell 2005). *F. rusticus* can also affect native fish assemblages through egg predation and by
130 altering habitat through extensive macrophyte destruction, thereby disrupting native food webs
131 (Capelli and Munjal 1982; Dorn and Mittelbach 1999; Kreps et al. 2016; Lodge et al. 1998;
132 Morse et al. 2013; Roth et al. 2007).

133 One of the mechanisms by which *F. rusticus* is believed to negatively affect native
134 species is through displacement from preferred habitats. Habitat associations of crayfish
135 communities have received very little attention, except perhaps in northern Wisconsin lakes
136 subject to rusty crayfish invasions (DiDonato and Lodge 1993; Garvey et al. 2003). Crayfish
137 habitat associations in lotic ecosystems, to our knowledge, have yet to be studied although some
138 information does exist at coarse spatial scales (Burskey and Simon 2010).

139 The quantity of streams and rivers in Michigan provides an opportunity to evaluate
140 crayfish habitat associations both with and without rusty crayfish present. Further, the past
141 distributional data reported by Lippson (1975) offers an opportunity to quantify how crayfish
142 communities in Michigan have changed through time and across space. This study seeks to a)
143 update our current understanding of the status and range of stream-dwelling crayfish within
144 Michigan's Upper and Lower Peninsula, b) identify habitat associations of crayfish species with
145 and without invasive rusty crayfish, c) document changes in the range of crayfish species
146 compared to historical data with an emphasis on non-native rusty crayfish, and d) evaluate the
147 effectiveness of our sampling method. With respect to b), we hypothesize that native species
148 will associate with less-desirable habitat in the presence of rusty crayfish at a given site. For c),
149 we hypothesize that rusty crayfish have expanded their range in Michigan over the last 40 years,
150 but native species have contracted their range owing to negative interactions with rusty crayfish.
151 We also provide an analysis of detectability given the uncertainty regarding our specific capture
152 method (dipnets), and to provide insight into the repeatability of this survey. Information
153 derived from this study will highlight large-scale trends in crayfish communities, and could assist
154 in prioritization of habitats for native crayfish conservation as well as locations to focus
155 prevention efforts for rusty crayfish. This study also adds to the growing body of literature
156 regarding indirect effects of invasions as related to how non-native species affect the habitat
157 selection of native species.

158

159 **Methods:**

160 *Crayfish collection*

161 Although crayfishes occupy two general habitat types – open water habitats and burrows
162 (Hobbs 1989) – this survey was limited to open water habitats of streams. We used the Michigan
163 Department of Natural Resources (MDNR) Stream Status and Trends Program (SSTP) (Seelbach
164 et al. 1997; Wills et al. 2006) to determine stream sampling sites. Stream segments were selected
165 by stratifying the SSTP database by management unit and major watershed. We selected at
166 random 20% of available stream segments for collection from each watershed stratum to evenly
167 distribute sampling effort across watersheds. Stream segments are inter-confluence stream
168 reaches, defined by tributary confluences or dams. The watershed stratum as defined in the
169 SSTP database were individual streams and their tributaries directly connected to a Great Lake
170 (Wills et al. 2006). All data were collected in summer of 2014-2016. We sampled 69 segments
171 in 2014, 277 segments in 2015, and 133 segments in 2016, for a total of 479 segments and 958
172 sites (two sites per segment) over the three year period of the study.

173 Technicians worked in pairs to sample stream segments at each site, and generally
174 attempted to access streams from a road crossing, with one individual working upstream and the

175 other downstream of the crossing. Technicians worked to catch as many crayfish as possible in a
176 20-minute period. We sampled crayfish with dip nets, using standard protocols for crayfish
177 collection (Olden et al. 2006). We selected dip nets because it allowed us to implement a
178 consistent sampling technique across all streams regardless of substrate type. This included
179 netting individuals off substrate, lifting rocks or larger substrate with the foot or hand, and using
180 hands and twigs to probe crayfish out of root structures or undercut banks. Collected crayfish
181 were temporarily retained for identification and measuring until dip netting was completed at a
182 site.

183 Once sampling at a site was complete, we recorded GPS coordinates at the center of each
184 sampling unit. After exiting the stream each crayfish was identified by species. Once crayfish
185 data were recorded, all rusty crayfish were euthanized whereas native crayfish were returned to
186 the stream.

187 *C. diogenes* and *C. polychromatus* were combined for all analyses due to their low catch
188 rates and difficulty in distinguishing young individuals. Because both species were formerly part
189 of a species complex (Thoma et al. 2005), data for the two were likely combined during
190 Lippson's survey and will be referred to as the '*diogenes* complex' in this paper (Lippson 1975;
191 Thoma et al. 2005).

192

193

194 *Habitat sampling*

195 Substrate characteristics were identified using a visual assessment of upstream and
196 downstream sampling areas. Substrate categories were based on a modified Wentworth scale and
197 included clay (<1/256 mm), silt (>1/256 mm, <1/16 mm), sand (>1/16 mm, <4 mm), pebble (>4
198 mm, <64mm), cobble (>64 mm, <256 mm), boulder (>256 mm), woody material (roots, tree
199 limbs, etc.), detritus, and living macrophytes (Wentworth 1922). Substrate was classified based
200 on amount present in each sampling area using a scale of 0%, 1-24%, 25-49%, 50-74%, and 75-
201 100%.

202

203 *Data and Statistical Analysis*

204

205 Detectability

206 We used occupancy analysis (e.g. Mackenzie et al. 2006) to analyze detect/non-detect
207 data from our survey of sites. These models provide probabilities associated with detecting an
208 individual species in either the same location through time (temporal detectability) or at proximal
209 sites within the same stream segment (spatial detectability). Temporal detectability models were
210 fit to pooled data of both technicians from 22 stream segments that were visited in 2014 and
211 again in 2015. This model tested whether a species would be detected at a location on every
212 occasion that it was sampled. Spatial detectability was modeled by comparing samples from the
213 same stream segment, i.e. one sample from upstream compared to the other from downstream of
214 the road crossing. This model tested whether crayfish assemblages were uniform throughout a
215 stream segment. Samples conducted on the same segment but at different times were treated as
216 their own unique sampling event, allowing a sample size of 479 comparisons for the spatial
217 model.

218 For this analysis, we made several assumptions consistent with previous applications (e.g.
219 Mackenzie et al. 2006). Foremost, we treated each observer as an independent survey visit, and
220 assumed that if the selected crayfish species was present within one observer's section, it was

221 present at the other. Put another way, we assumed that the occupancy status (i.e., present or
222 absent) applied to both sub-sites sampled. This assumption is critical for the occupancy analysis
223 and implies that if one searcher detects a crayfish species at a site, and the other observer does
224 not, this is due to a non-detection, thus allowing the analysis to provide estimates of detection
225 probability. Two other assumptions were that crayfish did not move into or out of a site within
226 the time to survey a site (i.e., the sites are closed during the time of the survey), and that crayfish
227 were identified accurately (i.e., no false positives).

228 The following occupancy model allowed us to obtain estimates of site occupancy as well
229 as detection probability {MacKenzie, 2002 #2175; Mackenzie, 2006 #2308}:

$$230 L(\psi, p) = (\psi^n \prod p_t^{n_t} (1 - p_t)^{n - n_t}) \times (\psi \prod (1 - p_t) + (1 - \psi))^{N - n}. \quad (1)$$

231 where t is the number of searchers at a site, N is the total number of sites surveyed, and n
232 is the number of sites where at least one detection occurred, ψ is the probability of occupancy, p
233 is the detection probability for a single searcher, and n_t is the number of detections on t^{th} survey.
234 We implemented this occupancy model and obtained estimates via the unmarked package in R (R
235 Core Team 2018).

236 Estimates of detection probability from this model are for a single searcher; we estimated
237 detectability for two searchers using the following equation:

$$238 p_d = 1 - (1 - p_s)^2 \quad (2)$$

239 where, p_d is the probability of detection with two searchers and p_s is the probability of detection
240 for a single searcher determined from the occupancy analysis.

241 Crayfish ranges

242 Crayfish presence/absence data were compared to Lippson's 1975 dissertation (Lippson
243 1975) to determine any changes in the range of crayfishes in Michigan. Lippson (1975)
244 presented their data in terms of successful captures for each species found at their sampling
245 locations. We assumed all species captured at a given site were reported, thus all non-reported
246 species were absent. We also compared changes in the co-occurrence of obligate aquatic species
247 (*C. robustus*, *F. propinquus*, *F. virilis*), as a result of increased *F. rusticus* ranges from previous
248 reports. Lippson's (1975) collections are reported at the county, township, range, and section
249 level. We converted the centroid of these locations to GPS coordinates, and then sorted
250 collections by United States Geological Survey (USGS) 8-digit Hydrologic Unit Code (HUC)
251 watersheds and MDNR Fisheries Management Units (FMU) (Michigan Department of Natural
252 Resources 2001; U.S. Department of Agriculture Service Center Agencies - National Geospatial
253 Management Center 2013). In this way, we were able to assign each of Lippson's sampling
254 locations to an 8-digit HUC watershed, for comparison to our survey data. Range maps were
255 constructed using shapefiles published by USDA/NRCS - National Geospatial Management
256 Center and the MDNR in ArcGIS version 10.1 (ESRI 2011; Michigan Department of Natural
257 Resources 2001; U.S. Department of Agriculture Service Center Agencies - National Geospatial
258 Management Center 2013).

259 Habitat associations

266 We used model selection to identify significant habitat predictors of presence or absence
267 for all crayfish species. We input habitat predictors into a generalized linear model (GLM) using
268 the logit function, and used backward selection using the stepAIC function of the MASS package
269 in R version 3.0.2(R Development Core Team 2008), to identify significant predictors. We
270 repeated this process for each species using the substrate classifications from the modified
271 Wentworth scale as covariates. Species were coded as 1 (present) or 0 (absent). Habitat
272 covariates were also coded as 0-4, corresponding to modified Wentworth scale abundance
273 classifications. We used a logit link function to fit the GLM. This allowed us to determine if the
274 presence of a crayfish species was positively or negatively associated with individual substrate
275 classes. Log odds ratio output from GLMs permitted us to identify the direction and magnitude
276 of effect, as any log odds value below 0 indicated lower than a 50% chance of finding a crayfish
277 associated with a given habitat, and values further away from 0 indicating larger effects. Log
278 odds ratios quantify the ratio of collecting a species to not collecting the species. Thus, if the
279 presence of a given habitat increases the odds of collecting the species, the ratio will increase,
280 and the log odds ratio will be greater than 0. To quantify changes in substrate associations based
281 on the presence or absence of *F. rusticus*, we ran separate analyses for each native species after
282 dividing samples into those where *F. rusticus* was present and those where *F. rusticus* was
283 absent. We used a significance level of $\alpha=0.05$ for all tests.

284

285

286 **Results:**

287

288 *Detectability*

289 The detectability of crayfish was high for obligate stream species both through time and
290 within individual segments. No obligate stream species had less than a 60% probability of
291 detection and most had detectabilities over 80% (Table 1). The primary and secondary burrowing
292 species showed lower detection probabilities, and temporal models for *C. fodiens* and *P. acutus*
293 could not be run due to lack of data, despite having moderate spatial detectability (46% and 67%,
294 respectively).

295

296 *Crayfish ranges*

297 During May-September of 2014-2016, crayfish species presence and absence was
298 assessed at 461 of the >2,000 unique stream segments in Michigan (Figure 1). Overall, all of
299 Michigan's native crayfish species were detected in more watersheds during this survey than in
300 1975 (Table 2). For *F. rusticus*, there is evidence for a substantial range expansion. We found *F.*
301 *rusticus* in 20% of samples and in 34 of 55 HUC 8 watersheds. By comparison, *F. rusticus* were
302 documented in only 12 HUC 8 watersheds in 1975 (Lippson 1975) (Table 2; Figure 2). Every
303 watershed that contained *F. rusticus* in 1975 also contained *F. rusticus* in this study (Figure 2).

304

305 Native species ranges appear to have shifted since 1975. Although we sampled more
306 watersheds than Lippson (1975), shifts in the overall range of some native species is apparent, as
307 well as changes in occurrence within some watersheds (Table 2). The most widely distributed
308 native species in our survey was *F. propinquus*, which we found in 48 of 55 HUC-8 watersheds
309 and 42% of samples. We found *F. propinquus* in three more watersheds than Lippson (1975), but
310 in a lower percent of samples (42 versus 72%) (Figure 3, top). When we only consider sites
311 where crayfish were collected, we found *F. propinquus* in 58% of samples, which still represents
a 14% decrease from Lippson (1975). The second most common native species found in this

312 survey was *F. virilis*, found in 43 watersheds and 20% of all samples, and 27% of samples that
313 contained crayfish. This represents a substantial increase in occurrence compared to Lippson
314 (1975), who only found *F. virilis* in 33 watersheds, but an identical percent of samples (27%)
315 (Figure 3, middle). *C. robustus* was found in 17 watersheds, and 5.8% of all samples and 8% of
316 samples that contained crayfish, making it the least common obligate aquatic crayfish species in
317 Michigan (Figure 3, bottom). We found *C. robustus* in five more watersheds compared to
318 Lippson (1975), who found this species in 6.4% of samples. We found *F. immunis* in 18
319 watersheds and 4.9% of all samples, and 6.8% of samples containing crayfish. Lippson (1975)
320 found *F. immunis* in eight fewer watersheds, but a similar percent of samples (5.5%) (Figure 4,
321 top). *P. acutus* was found in 3 watersheds and <1% of samples, making it the least common
322 crayfish in Michigan, limited to a few southern watersheds (Figure 4, bottom). Lippson (1975)
323 did not find *P. acutus* in any samples. The *diogenes* complex was found in 23 watersheds and
324 5.4% of all samples, and 7.4% of samples containing crayfish. Lippson (1975) only found *C.*
325 *diogenes* in 3.4% of samples, and in 15 fewer watersheds than the present study (Figure 5, top).
326 *C. fodiens* was found in 9 watersheds and 1.3% of all samples, and in 1.8% of samples
327 containing crayfish. *C. fodiens* was also rare in Lippson (1975), and was only found in 1.5% of
328 samples, although we found this species in six more watersheds (Figure 5, bottom).

329 Although we found all crayfish species in more watersheds compared to Lippson (1975),
330 we could not detect all species in locations where they were found historically. In terms of
331 facultative burrowing crayfish, we were unable to detect the *diogenes* complex in one watershed
332 that it was reported in 1975, *C. fodiens* was not detected in one watershed it was detected in
333 1975, and *F. immunis* was not detected in four watersheds where it was detected in 1975. For the
334 obligate stream species, we did not detect *C. robustus* in two watersheds that Lippson (1975) did,
335 *F. propinquus* was not detected in three watersheds it was formerly detected in 1975, and *F.*
336 *virilis* was not detected in six watersheds that it was detected in 1975.

337 The co-occurrence between obligate aquatic species and *F. rusticus* did not substantially
338 change from Lippson (1975), except for the reduced occurrence of *F. propinquus* in areas
339 occupied by *F. rusticus* (Table 3). We found *F. propinquus* co-occurring with *F. rusticus* in 23%
340 of samples, which represents a substantial decrease from Lippson (1975) who found *F.*
341 *propinquus* in 43% of samples that contained *F. rusticus*. In contrast *F. virilis* was found in 16%
342 of samples that contained *F. rusticus* in 1975, and 15% of samples in 2014-2016. *C. robustus*
343 was found in 8% of samples that contained *F. rusticus* in 1975 and 10% of samples in 2014-
344 2016. We also found similar co-occurrences of *C. robustus* with other species across studies. *F.*
345 *propinquus* was present in 62% of *C. robustus* samples in both 1975 and 2014-2016. *F. rusticus*
346 was in 12% of *C. robustus* samples in 1975, and 16% of samples in 2014-2016. *F. virilis* was in
347 12% of *C. robustus* samples in 1975, and 18% of samples in 2014-2016. At sites where *F.*
348 *propinquus* was found, it co-occurred with *F. rusticus* in 6% of samples in 1975 and 9% in 2014-
349 2016. *F. virilis* occurred in 20% of samples in both 1975 and 2014-2016. *C. robustus* occurred in
350 6% of samples in 1975, and 9% of samples in 2014-2016.

351

352 *Habitat Associations*

353 Model selection results for the substrate covariates and their effect on species presence
354 were successfully calculated for all species except for *P. acutus* due to small sample size (Table
355 4). The best model for the burrowing species *C. fodiens* only contained detritus, but this species
356 was strongly positively associated with this substrate (Log odds ratio = 0.75, $z = 3.83$, $p < 0.0001$;
357 Table 4). The *C. diogenes* complex was also positively associated with detritus (Log odds ratio

358 = 0.46, $z = 3.56$, $p = 0.0004$), but the best model for this species also contained boulder although
359 this variable was not significant (Log odds ratio = -1.06, $z = -1.263$, $p > 0.1$). *F. immunis*, which
360 is known to burrow but is more often found in slow waters with live vegetation, was found to be
361 positively associated with silt (Log odds ratio = 0.33, $z = 3.47$, $p < 0.001$) and live vegetation
362 (Log odds ratio = 0.28, $z = 2.29$, $p = 0.02$), which agrees with the life history of this species
363 (Lippson 1975; Tack 1939; Taylor et al. 2015).

364 Substrate associations of obligate stream dwelling species also agreed with literature
365 descriptions of their life history, for the most part. Model selection for *C. robustus* indicated
366 positive associations for silt, sand, pebble, cobble, boulder, and wood (all $p < 0.02$ except for
367 boulder which was not significant)(Table 4) *F. propinquus* demonstrated strong positive
368 associations with cobble, pebble, and sand (all $p < 0.001$), and *F. virilis* with live vegetation (Log
369 odds ratio = 0.30, $z = 4.332$, $p < 0.001$), detritus (Log odds ratio = 0.23, $z = 2.23$, $p = 0.026$), and
370 silt (Log odds ratio = 0.13, $z = 2.28$, $p = 0.023$), which agrees with descriptions of their life
371 history (Hobbs and Jass 1988; Lippson 1975; Taylor et al. 2007; Taylor et al. 2015). The best
372 model for invasive *F. rusticus* contained clay, cobble, and boulder (Table 4), although only the
373 latter two were significant (Cobble: Log odds ratio = 0.38, $z = 6.67$, $p << 0.001$; Boulder: Log
374 odds ratio = 0.35, $z = 2.988$, $p = 0.002$).

375 Evidence of the impact of rusty crayfish on native species was supported by an analysis
376 that separated samples where *F. rusticus* co-occurred with native species from those where *F.*
377 *rusticus* was absent. The analysis indicated shifts in substrate associations for some species when
378 *F. rusticus* was present (Table 5). The best model for *C. robustus* presence in the absence of
379 rusty crayfish contained a variety of substrates (silt, sand, pebble, cobble, boulder, and wood),
380 with the first four of these significant predictors (all $p < 0.02$). However, in the presence of rusty
381 crayfish, *C. robustus* was only positively associated with cobble and wood, with wood being the
382 sole significant predictor (Log odds ratio = 1.56, $z = 2.86$, $p = 0.004$). The best model for *F.*
383 *immunis* in the absence of *F. rusticus* contained positive associations with clay, silt, sand,
384 detritus, and live vegetation, with silt being the only significant predictor of *F. immunis* presence
385 at a given site (Log odds ratio = 0.49, $z = 3.048$, $p = 0.002$; all others $p > 0.06$)(Table 5).
386 However, when *F. rusticus* was present, vegetation was the only positive association with *F.*
387 *immunis*, and this variable was not significant (Log odds ratio = 0.44, $z = 1.66$, $p = 0.10$). The
388 best model for *F. immunis* in the presence of *F. rusticus* also contained negative associations
389 with sand, pebble, and cobble, with sand being the only significant variable in the best model
390 (Log odds ratio = -0.54, $z = -2.12$, $p = 0.03$; all others $p > 0.06$). *F. propinquus* shifted from a
391 best model with significant, positive associations with cobble, pebble, and sand (cobble: Log
392 odds ratio = 0.36, $z = 5.8$, $p < 0.001$; pebble: Log odds ratio = 0.19, $z = 2.86$, $p = 0.004$; sand: Log
393 odds ratio = 0.27, $z = 5.26$, $p < 0.001$) in the absence of *F. rusticus* to a best model with only one
394 significant positive association, with live vegetation, when *F. rusticus* were present (Log odds
395 ratio = 0.48, $z = 2.35$, $p = 0.02$). Other, non-significant habitat associations of *F. propinquus*
396 include positive associations with clay, pebble, and detritus, and negative associations with silt
397 and boulder. All these variables were not significant (all $p > 0.05$), although the negative
398 association with silt was marginally significant (Log odds ratio = -0.4, $z = -1.9$, $p = 0.06$) (Table
399 5). *F. virilis* showed relatively little change in the presence of rusty crayfish. Without *F.*
400 *rusticus*, the best model for *F. virilis* contained a negative association with sand (Log odds ratio
401 = -0.21, $z = -3.22$, $p = 0.001$) and a positive association with vegetation (Log odds ratio = 0.21, z
402 = 2.75, $p = 0.006$). The best model with *F. rusticus* only contained vegetation, although this
403 predictor was not significant (Log odds ratio = 0.31, $z = 1.48$, $p > 0.1$).

404

405 **Discussion:**

406 The introduction and subsequent spread of non-native species, and their consequent
407 effects on native fauna, is a central issue in the conservation of biodiversity. Research to inform
408 the management of aquatic invasions needs to combine mechanistic, typically small-scale,
409 studies of invasive species to understand how the invaders cause negative effects on native
410 species, with broad-scale investigations of invasion spread and ecosystem response. The study
411 reported here focuses on this latter component, combining an extensive survey of contemporary
412 crayfish distributions in Michigan with observations of habitat association shifts in native
413 crayfish species in response to the presence of an invader – the rusty crayfish. Our research
414 complements a similarly broad-scale study in crayfish distribution changes in Wisconsin (Olden
415 et al. 2006) and Illinois (Taylor and Redmer 1996) and adds evidence for effects of rusty crayfish
416 on habitat use by native crayfish. Rusty crayfish have been intensively studied, and their impact
417 on native fauna in individual systems has been well-documented, particularly in northern
418 Wisconsin lakes (e.g. Roth et al. 2007; Wilson et al. 2004). There is some prior evidence of the
419 effect of their geographical spread on the distribution of native crayfishes (Olden et al 2006). Our
420 study adds substantially to this record, and also provides evidence for a potential mechanism for
421 these effects – namely displacement of native crayfishes into less preferred habitats. Broad-scale
422 research of this type provides a valuable foundation for both documenting the extent of an
423 invasion’s impact on native ecosystems, and suggesting hypotheses about mechanisms giving
424 rise to the observed patterns that can subsequently become the focus of more mechanistic
425 investigations.

426

427 *Ranges of Michigan crayfishes*

428 Native crayfish species remain broadly distributed across Michigan, but we found
429 evidence of an ongoing expansion of *F. rusticus* from previous surveys (Creaser 1931; Lippson
430 1975). The increase in *F. rusticus* range concomitant with a decrease in co-occurrence with *F.*
431 *propinquus* suggests that *F. rusticus* locally displace *F. propinquus*, consistent with previous
432 literature. *F. rusticus* are known to hybridize with *F. propinquus*, which acts to shift the genetic
433 and phenotypic population toward characteristics exhibited by *F. rusticus* (Capelli and Munjal
434 1980; Perry et al. 2002; Perry et al. 2001b). Antagonistic interactions between native crayfishes
435 and *F. rusticus* likely exacerbate rusty crayfish invasions (Mather and Stein 1993a, b), and give
436 rise to habitat use shifts, as discussed below. Previous work has shown that *F. rusticus*
437 outcompete both *F. propinquus* and *F. virilis* for habitat, while exhibiting lower susceptibility to
438 native predators (Bergman and Moore 2003a, b; Capelli and Munjal 1982; DiDonato and Lodge
439 1993; Garvey et al. 2003; Hill and Lodge 1994; Roth and Kitchell 2005). Our findings are
440 consistent with these studies given the shift in *F. propinquus* associations away from preferred
441 cobble and woody debris toward vegetation. The exclusion of *F. propinquus* from preferred
442 habitat could make them more susceptible to predation, or place them in suboptimal habitat for
443 growth. However, more research must be conducted to quantify predation on *Faxonius*
444 crayfishes in stream habitats and the role of predation in species displacement, as previous
445 studies were conducted in lakes (e.g. DiDonato and Lodge 1993; Garvey et al. 2003; Roth and
446 Kitchell 2005).

447 Differences in watershed-level species presence-absence between our survey and
448 Lippson’s earlier survey may have arisen for multiple reasons. First, our sampling effort, at least
449 in terms of the number of sites where crayfish were captured, was substantially greater than

450 Lippson's (694 vs 326). Second, either survey could have failed to detect a species in a
451 watershed where they were actually present, particularly if the habitat preferred by a species was
452 not observed at the sites where samples were collected, but was in fact present in the watershed.
453 Third, in-stream biochemical and habitat conditions have likely changed in some watersheds
454 over the past 40 years, so that our sampling detected actual changes in species ranges due to
455 habitat change. Finally, as noted above the distributions of some native species may have
456 changed as a consequence of the increased range of *F. rusticus*. The relative importance of these
457 factors in explaining observed changes in native species distributions will require further study.

458

459 *Habitat associations of Michigan crayfishes*

460 Previous studies indicate that *F. virilis* adults (in isolation) prefer rocky substrates, and
461 macrophyte beds are important nursery habitat for young (Crocker and Barr 1968; France 1985;
462 Momot and Gowing 1983). Although *F. virilis* is often considered a habitat generalist, it is
463 vulnerable to exclusion from preferred habitat types as a result of competition, particularly with
464 congeners *F. propinquus* and *F. rusticus* (Hobbs and Jass 1988; Lippson 1975; Peck 1985;
465 Taylor et al. 2015). In this study, *F. virilis* demonstrated an affinity for cobble and a negative
466 association with sand in the absence of both *F. propinquus* and *F. rusticus*. However, in areas
467 where *F. virilis* co-occur with either *F. propinquus* or *F. rusticus* we observed that *F. virilis* was
468 positively associated with vegetation and silt, and was no longer associated with cobble (Table
469 6). Further community change could arise if *F. rusticus* has a negative effect on macrophyte
470 beds, thus eliminating the remaining refuge for *F. virilis* and *F. propinquus* (Lodge and Lorman
471 1987; Roth et al. 2007). Prior to *F. rusticus* invasion, *F. propinquus* and *F. virilis* likely lived in
472 preferred habitat in the absence of the other, with *F. virilis* persisting in vegetative habitat when
473 the two co-occurred (Garvey et al. 2003; Hill and Lodge 1994; Peck 1985). This still appears to
474 be the case in many locations. However, when *F. rusticus* excludes *F. propinquus* from cobble,
475 areas where the three species overlap could result in the eventual removal of *F. virilis*.

476 *C. robustus* appeared largely unaffected by *F. rusticus* despite preferring large coarse
477 substrates. This finding is consistent with Berrill (1978), suggesting that unknown differences in
478 behavior or ecological roles might allow *C. robustus* to co-occur with *F. rusticus* and other
479 members of *Faxonius spp.* This result is echoed by Reid and Nocera (2015), which indicate that
480 *C. robustus* may occupy a unique niche compared to *Faxonius* species. However, a report by
481 Daniels (1998) suggests that *F. rusticus* might be displacing *C. robustus* in an Ontario watershed.
482 Our data suggests that since 1975 the cohabitation of *C. robustus* and the other obligate aquatic
483 species, including *F. rusticus*, is stable. This further suggests that there are determinants that
484 influence the coexistence between *C. robustus* and *Faxonius spp.* other than substrate. Berrill et
485 al. (1985) indicate that low pH conditions could be favorable to *C. robustus*, but the vast
486 majority of rivers in Michigan have pH levels >7.0 (<https://waterdata.usgs.gov/mi/>), which is
487 above the threshold of 5.5 described in Berrill et al. (1985).

488 We did not observe any negative effects of *F. rusticus* on native burrowing species.
489 Generally, burrowing species tended to prefer silt or detritus substrates, which *F. rusticus* did not
490 prefer in our study. The lack of influence of *F. rusticus* on the presence of these species is likely
491 due in part to their differing life histories. The ability of burrowing species to occupy temporary
492 water bodies and construct semi-terrestrial burrows likely excludes them from much of the
493 shelter competition faced by obligate aquatic species. However, there is a void in literature
494 relating to the relationships between these species and *F. rusticus*.

495

496 *Detectability*

497 Exclusively sampling streams likely resulted in the under-reporting of Michigan's
498 burrowing crayfish despite their need to enter water during the spring to release young into the
499 water (Hobbs and Jass 1988; Lippson 1975). Although we observed burrowing species in more
500 watersheds than Lippson (1975), caution should be used when interpreting this result as a range
501 expansion due to our lack of understanding regarding the specific methods used to capture
502 burrowing crayfish in Lippson (1975). Lippson (1975) indicates that he used a variety of
503 methods including dipnets, seines, burrow excavation, and baited traps, but he was unspecific
504 about which method was used to capture individual specimens or species. The current
505 conservation status of burrowing crayfish in Michigan, and in many other locales, is unknown
506 (Taylor et al. 2007). We suggest conducting further surveys aimed at more accurately depicting
507 the range, habitat associations, and status of burrowing species to gain a fuller understanding of
508 burrowing crayfish populations in the state. Surveys could include ephemeral waterbodies, wet
509 meadows, roadside ditches, burrows near streams and ponds, and any other wetlands. Little is
510 known on the status of burrowing species in the state and no extensive work has been done since
511 *C. polychromatus* was described, separating it as a species apart from *C. diogenes* (Thoma et al.
512 2005). An evaluation of burrowing crayfish is particularly relevant given the recent detection of
513 red swamp crayfish (*P. clarkii*) in multiple locations in Michigan (Smith et al *in press*). All
514 discoveries were in the southern portion of the state in lentic waterbodies (lakes or retention
515 ponds) that were not the focus of the study. However, the discovery of this highly invasive
516 species is concerning not only for the conservation of burrowing crayfish, but for all crayfish
517 species and aquatic food webs as a whole.

518 Overall our methods of dip netting appear to have sufficiently sampled streams for
519 obligate aquatic species of crayfish. Dip netting allowed us to sample all substrate types within
520 flows typical of wading streams. Dip netting also removed the possibility of sample bias related
521 to habitat preferences and sex-specific behavior (Hill and Lodge 1994; Olden et al. 2006; Price
522 and Welch 2009; Smily and Dibble 2000) Passive methods of capture, such as trapping, results
523 in a bias toward males of more aggressive species and might result in different catch rates in
524 different waterbodies based on predator densities (Collins et al. 1983; Dorn et al. 2005). Other
525 studies have stated detection probabilities upwards to 88% for throw traps (Dorn et al. 2005),
526 68% for electroshocking, 38% for trapping, and dip netting as low as 32% (for one half hour)
527 (Price and Welch 2009). Our detectability model showed that dip netting appeared to be an
528 effective method of detecting crayfish in a stream. For obligate aquatic species, spatial or
529 temporal detectability was never below 60%, which is substantially higher than the other studies.

530
531 *Conclusion*

532 This study presents evidence that rusty crayfish have continued to expand their
533 distribution in the state Michigan since the last comprehensive survey more than 40 years ago,
534 based on a systematic and representative survey of catchments throughout the state. We also
535 found that habitat selection by the two most widespread native species, *F. propinquus* and *F.*
536 *virilis*, shifts when the invasive *F. rusticus* is present, suggesting a mechanism for biogeographic
537 effects of this invader on native crayfishes. Our study provides a model for broad-scale
538 investigations of the spread and effects of an aquatic invasive species, and helps to guide more
539 intensive, mechanistic investigations into the causes of invasive species impacts on native
540 species, ideally leading to advice on strategies for mitigating the negative effects of invaders.

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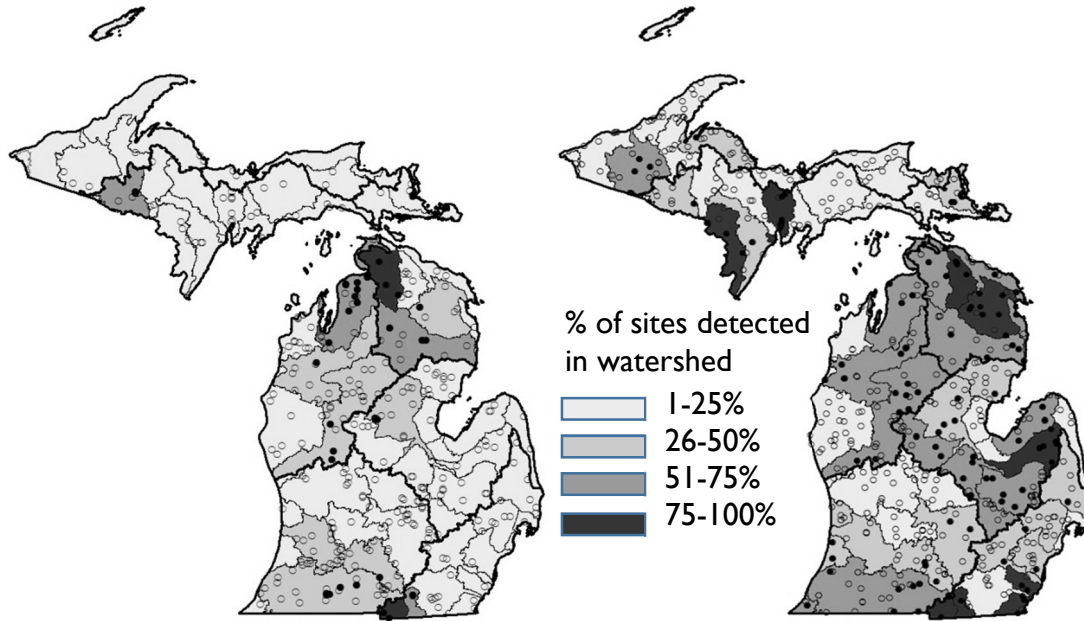
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764 Figure 1. Stream segments sampled from 2014-2016. Each dot represents one paired sample.

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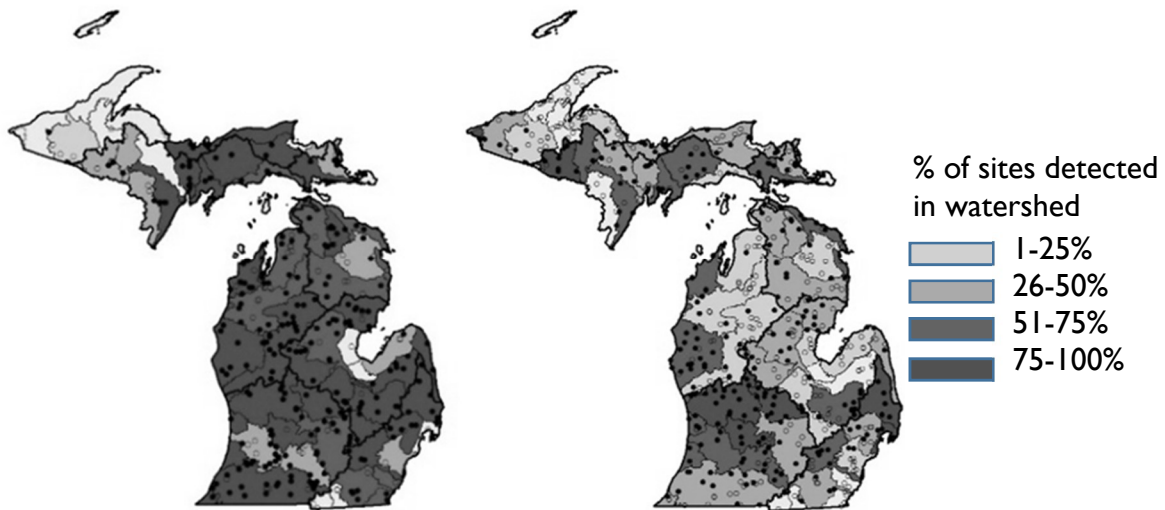


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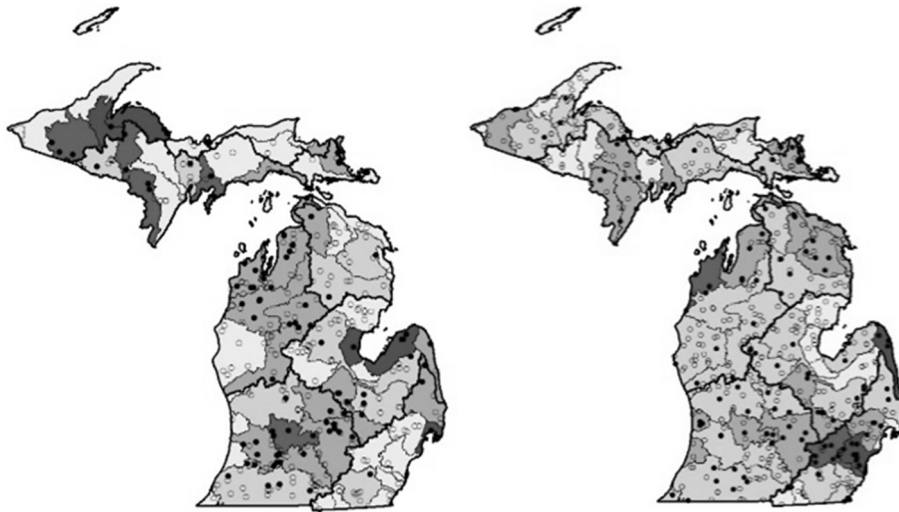
767 Figure 2. Distribution of rusty crayfish in 1975 (L) and 2014-2016 (R). Closed circles indicate
 768 where *F_O. rusticus* was found, open circles denote locations where *F_O. rusticus* was not
 769 detected.

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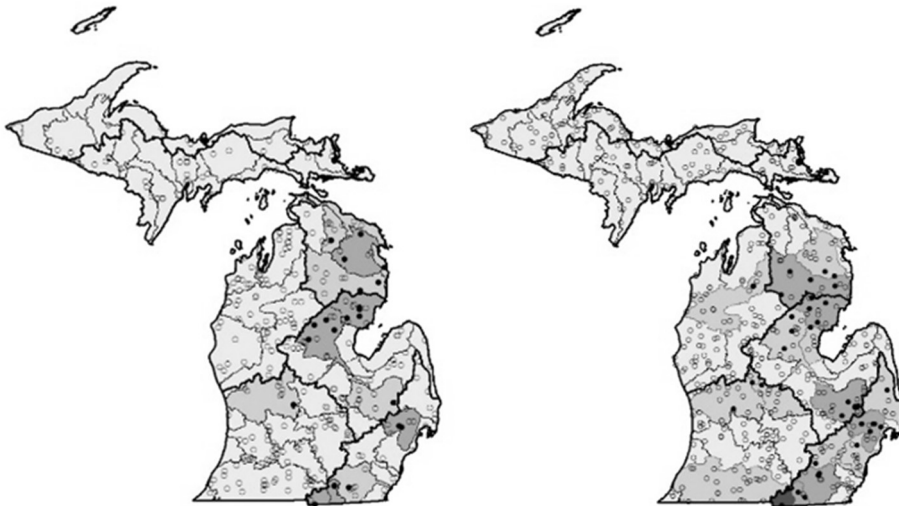
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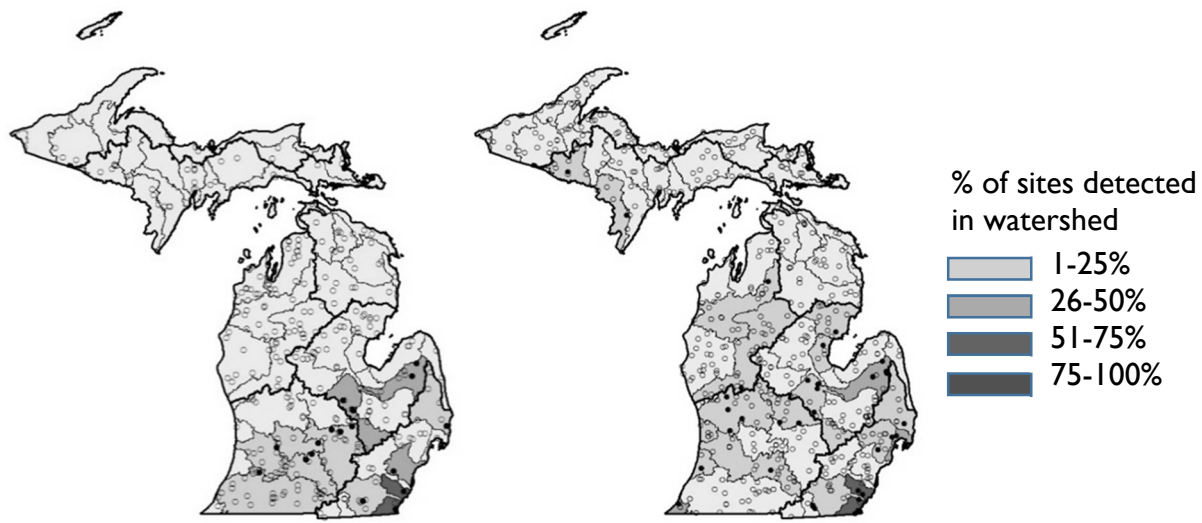


774 Figure 3. Distribution maps of obligate aquatic species, *FQ. propinquus* (top), *FQ. virilis*
775 (*middle*), and *C. robustus* (bottom) from Lippson (1975) (left) and 2014-2016 (right). Closed

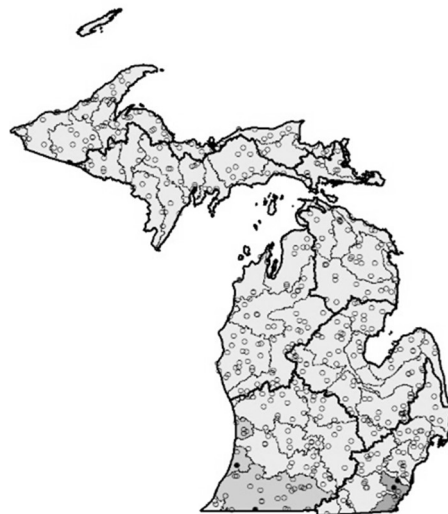
776 circles indicate where specimens were found, open circles denote locations where specimens
777 were not detected.

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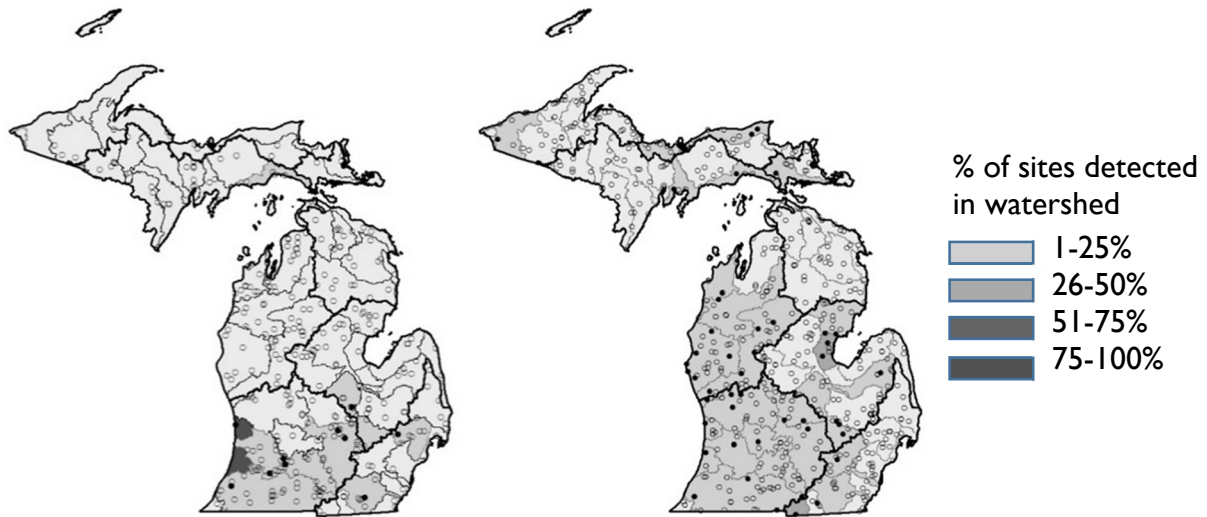
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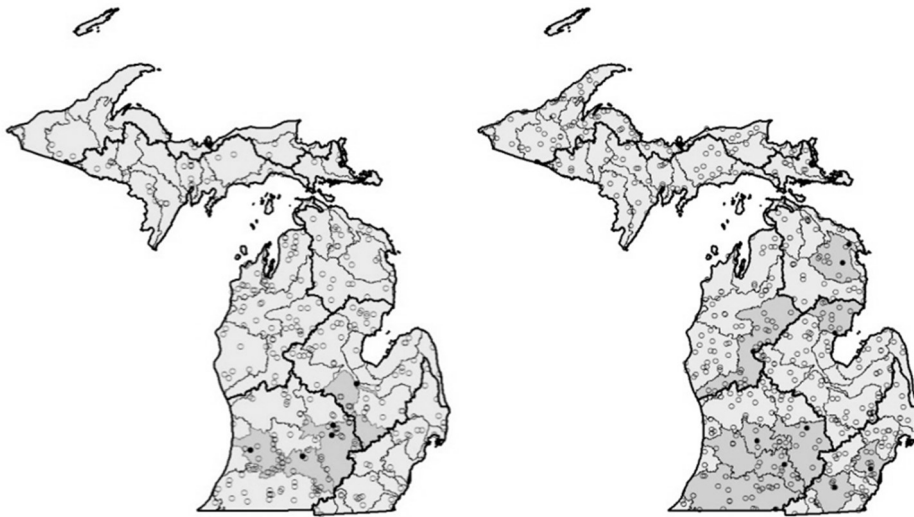
783 Figure 4. Distribution map of facultative burrowing species *Fθ. immunis* (top) and *P. acutus*
784 (bottom). Data for *Fθ. immunis* is present from Lippson (1975) (left) and 2014-2016 (right),
785 whereas no *P. acutus* were found in Lippson (1975). Closed circles indicate where specimens
786 were found, open circles denote locations where specimens were not detected.

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791 Figure 5. Distribution maps of obligate burrowing species, *C. diogenes* (top) and *C.F. fodiens*
 792 (bottom) from Lippson (1975) (left) and 2014-2016 (right). Closed circles indicate where
 793 specimens were found, open circles denote locations where specimens were not detected.

794

795 Table 1: Detectability of crayfish species during 2014-2015 stream surveys over time and space.
 796 ψ being occupancy and P being probability of detection.

Species	Spatial Detectability		Temporal Detectability	
	Ψ	P	Ψ	P
<i>C. diogenes</i>	0.289	0.222	0.182	0.500
<i>C. robustus</i>	0.132	0.607	0.142	0.800
<i>C. fodiens</i>	0.040	0.462	-	-
<i>F. immunis</i>	0.121	0.533	0.182	0.500
<i>F. propinquus</i>	0.548	0.826	0.683	0.966
<i>F. rusticus</i>	0.283	0.852	0.230	0.889
<i>F. virilis</i>	0.354	0.609	0.371	0.857
<i>P. acutus</i>	0.013	0.667	-	-
	n=350		n=22	

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801 Table 2: Crayfish occurrence by HUC8 watershed (n=55). A comparison of occurrences reported
802 in a 1975 survey and findings during 2014-2016 field sampling. Specific watersheds
803 occurrences are located in the Appendix.

Species	1975	2016
<i>C. diogenes</i>	8	23
<i>C. robustus</i>	12	17
<i>C. fodiens</i>	3	9
<i>F. immunis</i>	10	18
<i>F. propinquus</i>	45	48
<i>F. rusticus</i>	12	34
<i>F. virilis</i>	33	43
<i>P. acutus</i>	0	3

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807 Table 3: Relative co-occurrence (%) of Michigan obligate stream-dwelling crayfish in samples of
 808 *C. robustus* (n=56 for this study), *F. propinquus* (n=405 for this study), and *F. rusticus*
 809 (n=198 for this study) for years 1975 and 2016 and the amount of change between years. It
 810 should be noted that the number of samples for 1975 is unknown.
 811

Co-occurring Species	Survey Species					
	<i>C. robustus</i>		<i>F. propinquus</i>		<i>F. rusticus</i>	
	1975	2016	1975	2016	1975	2016
<i>C. robustus</i>			6	9	8	10
<i>F. propinquus</i>	62	62			43	23
<i>F. rusticus</i>	12	16	6	9		
<i>F. virilis</i>	12	18	20	20	16	15

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815 Table 4: Summarized generalized linear model results showing statistically significant
 816 relationships for crayfish species presence or absence based on habitat. Potential covariates were
 817 clay, silt, sand, pebble, cobble, boulder, wood, detritus, and live vegetation. Asterisks indicate
 818 significance at $p < 0.05$ (*), < 0.01 (**), < 0.001 (***)

	log Odds (Std. Error) <i>C. diogenes</i>	log Odds (Std. Error) <i>C. robustus</i>	log Odds (Std. Error) <i>C. fodiens</i>	log Odds (Std. Error) <i>F. immunis</i>
(Intercept)	-2.99 (0.17)***	-5.60 (0.77)***	-4.78 (0.36)***	-3.58 (0.25)***
Clay				
Silt		0.59 (0.20)**		0.33 (0.10)***
Sand		0.42 (0.17)*		
Pebble		0.47(0.18)**		
Cobble		0.83 (0.17)***		
Boulder	-1.06 (0.84)	0.48(0.27)		
Wood		0.94 (0.29)**		
Detritus	0.46 (0.13)***		0.75 (0.20)***	
Live Veg.				0.28 (0.12)*
	<i>F. propinquus</i>	<i>F. rusticus</i>	<i>F. virilis</i>	
(Intercept)	-1.00 (0.13)***	-1.90 (0.12)***	-1.80 (0.12)***	
Clay		-0.56 (0.47)		
Silt			0.13 (0.06)*	
Sand	0.26 (0.05)***			
Pebble	0.21 (0.16)***			
Cobble	0.18 (0.05)***	0.38 (0.06)***		
Boulder		0.35 (0.11)**		
Wood				
Detritus			0.23 (0.10)*	
Live Veg.			0.30 (0.07)***	

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822 Table 5. Comparison of generalized linear model results where habitat predictors of crayfish species presence or absence is influenced
 823 by the presence or absence of *QF. rusticus*.

<i>C. robustus</i>		<i>F. propinquus</i>	
	<i>F. rusticus</i> present	<i>F. rusticus</i> absent	
	log Odds (Std. Error)	log Odds (Std. Error)	
(Intercept)	-4.33(0.80)***	-5.33(0.80)***	(Intercept) -1.78(0.33)***
Clay			Clay 8.17(441.3)
Silt		0.56(0.21)**	Silt -0.40(0.21)
Sand		0.39(0.18)*	Sand
Pebble		0.42(0.19)*	Pebble 0.27(0.16)
Cobble	0.45(0.27)	0.83(0.17)***	Cobble
Boulder		0.51(0.30)	Boulder -0.55(0.44)
Wood	1.56(0.54)**	0.62(0.37)	Wood
Detritus			Detritus 0.52(0.29)
Live Veg.			Live Veg. 0.48(0.20)*
<i>F. immunis</i>		<i>F. virilis</i>	
	<i>F. rusticus</i> present	<i>F. rusticus</i> absent	
	log Odds (Std. Error)	log Odds (Std. Error)	
(Intercept)	-1.46(0.61)*	-4.52(0.61)***	(Intercept) -1.96(0.25)***
Clay		0.61(0.33)	Clay
Silt		0.49(0.16)**	Silt
Sand	-0.54(0.26)*	0.25(0.18)	Sand
Pebble	-1.00(0.53)		Pebble
Cobble	-0.33(0.21)		Cobble
Boulder			Boulder
Wood			Wood
Detritus		0.40(0.22)	Detritus
Live Veg.	0.44(0.27)	0.30(0.18)	Live Veg. 0.31(0.21)

825 Table 6: GLM output for substrate co-variate effect on *OE. virilis* presence when *OE.*
 826 *propinquus* and *OE. rusticus* were absent compared to when either *OE. propinquus* or *OE.*
 827 *rusticus* were present in samples.

	FR and FP absent	FR and FP present
(Intercept)	-1.46 (0.30)***	-1.89 (0.15)***
Clay		
Silt		0.15 (0.09)*
Sand	-0.29 (0.11)**	
Pebble		
Cobble	0.31 (0.12)**	
Boulder	-0.73 (0.45)	
Wood	0.58 (0.31)	
Detritus	0.22 (0.13)	
Live Veg.	0.22 (0.11)	0.34 (0.10)***

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831 Table A1. Crayfish occurrence by HUC8 watershed (n=55). A comparison of occurrences reported in a 1975 survey and findings
 832 during 2014-2016 field sampling.

HUC8	Watershed	L. diogenes		C. robustus		F. fodiens		F. immunis		F. propinquus		F. rusticus		F. virilis		P. acutus	
		1975	2016	1975	2016	1975	2016	1975	2016	1975	2016	1975	2016	1975	2016	1975	2016
	Sum	8	23	12	17	3	9	10	18	45	48	12	34	33	43	0	3
4080101	Au Gres-Rifle		x	x	x		x		x	x	x		x				
4070007	Au Sable			x	x					x	x	x	x	x	x		
4010302	Bad-Montreal										x						
4060104	Betsie-Platte		x							x	x			x	x		
4020201	Betsy-Chocolay		x							x	x				x		
4080104	Birch-Willow									x	x			x	x		
4070005	Black			x						x	x		x		x		
4050002	Black-Macatawa	x	x					x		x	x		x		x		x
4020101	Black-Presque Isle		x								x				x		
4060105	Boardman-Charlevoix									x	x	x	x	x	x		
4060107	Brevoort-Millecoquins	x	x							x	x			x	x		
4030106	Brule							x		x	x	x	x	x			
4070002	Carp-Pine		x							x	x					x	
4080205	Cass		x					x	x	x			x	x			
4030109	Cedar-Ford									x	x		x		x		
4070004	Cheboygan									x	x	x	x	x	x		
4090003	Clinton	x		x	x			x		x	x		x		x		
4020105	Dead-Kelsey										x		x	x	x		
4090004	Detroit				x		x	x		x	x		x		x		
4030110	Escanaba										x				x		
4030112	Fishdam-Sturgeon		x							x	x			x	x		
4080204	Flint			x	x					x	x		x	x	x		
4090005	Huron		x		x					x	x		x		x		
4050003	Kalamazoo	x	x			x	x	x	x	x	x	x	x	x	x		
4080102	Kawkawlin-Pine		x		x					x		x			x		
4020103	Keweenaw Peninsula																
4090002	Lake St. Clair								x		x			x			
4040001	Little Calumet-Galien								x	x	x		x		x		
4070003	Lone Lake-Ocqueoc			x						x	x		x		x		
4050006	Lower Grand		x	x	x				x	x	x			x	x		
4060103	Manistee		x		x					x	x	x	x	x	x		
4060106	Manistique									x	x				x		

Table A1 cont.

HUC8	Watershed	L. diogenes		C. robustus		F. fodiens		F. immunis		F. propinquus		F. rusticus		F. virilis		P. acutus	
4050005	Maple		x		x				x	x	x			x	x		
4030108	Menominee								x	x			x	x	x		
4030107	Michigamme									x	x			x			
4060102	Muskegon		x				x		x	x	x	x	x	x	x		
4020102	Ontonagon									x	x		x	x	x		
4100001	Ottawa-Stony							x	x	x			x		x		x
4060101	Pere Marquette-White		x							x	x				x		
4080103	Pigeon-Wiscoggin									x	x		x	x	x		
4080202	Pine									x	x		x		x		
4100002	Raisin	x	x	x	x		x	x	x	x	x			x	x		
4080203	Shiawassee	x	x			x		x	x	x	x		x	x	x		
4090001	St. Clair				x			x	x	x	x		x	x	x		
4050001	St. Joseph 1	x	x		x		x	x		x	x	x	x	x	x		x
4100003	St. Joseph		x	x	x							x	x				
4070001	St. Marys									x	x		x	x	x		
4020104	Sturgeon													x	x		
4030111	Tacoosh-Whitefish									x	x		x	x			
4020202	Tahquamenon									x	x						
4050007	Thornapple		x				x	x		x	x			x	x		
4070006	Thunder Bay			x	x		x			x	x	x	x	x	x		
4100006	Tiffin			x	x							x	x				
4080201	Tittabawassee			x	x					x	x	x	x	x	x		
4050004	Upper Grand	x	x			x	x	x		x	x		x	x	x		

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